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a unified framework for understanding variation in terrestrial biodiversity

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PERSPECTIVES

Ecospace: A unified framework for understanding variation in terrestrial biodiversity

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Abstract

Understanding patterns in biodiversity is a core ambition in ecological research. Existing ecological theories focusing on individual species, populations, communities, or niches aid in understanding the determinants of biodiversity patterns, yet very few general models for biodiversity have emerged from simplistic approaches. We propose that a systematic, low-dimensional representation of environmental space with building blocks adopted from gradient, niche, metapopulation and assembly theory may unite old and new aspects of biodiversity theory and improve our understanding of variation in terrestrial biodiversity.

We propose the term *ecospace* to cover the local conditions and resources underlying diversity. Our definition of ecospace encompasses abiotic *position*, biotic *expansion* and spatiotemporal *continuity*, which all affect the biodiversity of a biotope (α-diversity). *Position* refers to placement along abiotic gradients such as temperature, soil pH and fertility, leading to environmental filtering known from classical community theory. *Expansion* represents the build-up and diversification of organic matter that are not strictly given by position. *Continuity* refers to the spatiotemporal extension of position and expansion.

Biodiversity is scale dependent. The contribution of one biotope to large scale diversity must be estimated by considering its unique contribution to the species richness of the surrounding landscape or region or to the biodiversity of the entire planet. In addition to the relationship between ecospace and biotope richness (α-diversity), we also propose a relation between the *uniqueness* of the biotope ecospace and the unique contribution of species to the surrounding larger-scale richness.

Whereas the impacts of ecospace position and continuity on biodiversity have been studied in isolation, studies comparing or combining them are rare. Furthermore, biotic expansion has never been fully developed as a determinant of biodiversity, ignoring the megadiverse carbon-depending groups of insects and fungi. Precursors of the ecospace concept have been presented over the last 70 years, but they were never fully developed conceptually for terrestrial biodiversity or applied to prediction of biodiversity.

Ecospace unites classical and – at times – contradicting theories such as niche theory, island biogeography theory and a suite of community assembly theories into one framework for further development of a general theory of terrestrial biodiversity.

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Zusammenfassung

Die Muster der Biodiversität zu verstehen ist ein zentrales Anliegen der ökologischen Forschung. Ökologische Theorien, die auf einzelne Arten, Populationen, Gemeinschaften oder Nischen zielen, helfen dabei, aber nur sehr wenige generelle Modelle zur Biodiversität sind aus einfachen Ansätzen hervorgegangen. Wir schlagen vor, dass eine systematische Darstellung des Umweltraumes mit wenigen Dimensionen, die Bausteine aus der Gradienten-, Nischen-, Metapopulations- und Gemeinschaftstheorie verwendet, alte und neue Aspekte der Biodiversitätstheorie vereinigen und unser Verständnis zur Variation terrestrischer Biodiversität verbessern könnte.

Wir schlagen den Begriff 'ecospace' vor, um die lokalen Bedingungen und Resourcen, die der Diversität zugrunde liegen, abzudecken. Diese Definition von 'ecospace' umfasst die abiotische 'position', die biotische 'expansion' und die raum-zeitliche 'continuity', die alle die Biodiversität (α-Diversität) eines Biotops beeinflussen.

'Position' bezieht sich auf die Lage entlang von abiotischen Gradienten (Temperatur, Boden-pH, Fruchtbarkeit), woraus sich eine Wirkung als Umweltfilter aus der klassischen Gemeinschaftstheorie ergibt. 'Expansion' beschreibt den Aufbau und die Diversifizierung organischer Substanz, die nicht durch die 'position' vorgegeben sind. 'Continuity' beschreibt die raum-zeitliche Ausdehnung von 'position' und 'expansion'.

Biodiversität ist skalenabhängig. Der Beitrag eines Biotops zur großräumigen Diversität muss bestimmt werden, indem sein besonderer Beitrag zum Artenreichtum der umgebenden Landschaft, der Region oder des Planeten berücksichtigt wird. Zusätzlich zur Beziehung zwischen 'ecospace' und Artenreichtum eines Biotops (α-Diversität), schlagen wir auch eine Beziehung zwischen der 'uniqueness' des 'ecospace' eines Biotops und seinem besonderen Beitrag an Arten zum großräumigen Artenreichtum vor. Während die Einflüsse von 'position' und 'continuity' auf die Biodiversität einzeln untersucht wurden, sind Studien, die sie vergleichen oder kombinieren, selten. Darüber hinaus ist biotische 'expansion' niemals vollständig als bestimmender Faktor für die Biodiversität ausgearbeitet worden, wobei die megadiversen heterotrophen Gruppen der Insekten und Pilze ignoriert wurden. Vorläufer des 'ecospace'-Konzepts hat es in den letzten 70 Jahren gegeben, aber sie wurden nie vollständig für die terrestrische Biodiversität entwickelt oder zur Vorhersage von Biodiversität eingesetzt.

Das 'ecospace'-Konzept vereinigt klassische und zuweilen einander wiedersprechende Theorien wie Nischentheorie, Theorie der Inselbiogeographie und eine Reihe von Theorien zur Gemeinschaftsbildung in einem Beziehungsgefüge zur weiteren Entwicklung einer allgemeinen Theorie der terrestrischen Biodiversität.

Introduction

Understanding variation in species diversity remains among the major questions facing science in our time (Pennisi 2005). Ecologists have struggled to explain the variation in biodiversity, but only few cross-taxon and cross-habitat theories are widely accepted – perhaps reflecting a classical atomistic focus in biodiversity research on specific selections of species, habitats or processes. As early as 1949, Elton (1949) called for a broader community approach incorporating all types of organisms and their habitats in order to enhance the overall understanding of community assembly and ecosystem function. Similarly, Southwood (1977) realized that no single theory could explain the complex patterns in nature and that theories therefore ought to be pluralistic. Despite great advances in our understanding of the importance of species pools (Svenning, Eiserhardt, Normand, Ordonez, & Sandel 2015; Zobel 1997), spatiotemporal continuity (Ovaskainen & Hanski 2001) and ecological gradients (Grace et al. 2016), we are still left with very few generally agreed principles or models explaining variation in

biodiversity. Fortunately, molecular techniques now allow us to gather the comprehensive cross-taxon biodiversity data needed for developing this field further (Bohmann et al. 2014; Yoccoz 2012). However, a template or framework for understanding and modeling the quantified variability in biodiversity is needed to complement the new techniques.

Here, we advocate for a general approach to understand local biodiversity, substituting single species habitat modeling with environmental mapping of both abiotic conditions and organic resources. We suggest 'ecospace' – shorthand for 'ecological space' – as term for an inclusive framework for biodiversity research and conservation. The basic idea has been outlined in classic works (e.g., Elton 1949; Southwood 1996), but has never been fully developed as a conceptual framework. Meanwhile, the term 'ecospace' has developed independently within paleoecology (Bambach 1983) to describe the possible and realized modes and forms of life in prehistoric and modern marine species assemblages (Bambach, Bush, & Erwin 2007; Novack-Gottshall 2007).

In our reinterpretation of Elton's and Southwood's works, ecospace is defined as the multidimensional and

spatiotemporal space of conditions and resources, in which terrestrial biodiversity develops. We define the geospatial basis for ecospace as a biotope, i.e. the physical area, in which a given set of organisms live. The term habitat, in contrast, is used to signify the set of environmental conditions matching the specific needs of a species or a group of species sharing the same niche (Udvardy 1959). Consequently, the ecospace framework can be used to immediately predict variation in α-diversity, and to assess the probable composition of species and, thus, the diversity contribution of a biotope to large-scale biodiversity. In theory, the framework is not limited to a fixed spatial scale, but there are inevitable trade-offs between homogeneity and representation. Ecospace is defined and mapped at biotope scale and represents a spatiotemporal projection of the major physicochemical conditions and realized pools of organic carbon. Every terrestrial biotope – regardless of its ecological setting and spatiotemporal extent – can be described in terms of its ecospace. We presume that the ecospace framework also works in aquatic environments although the spatial delimitation of a given
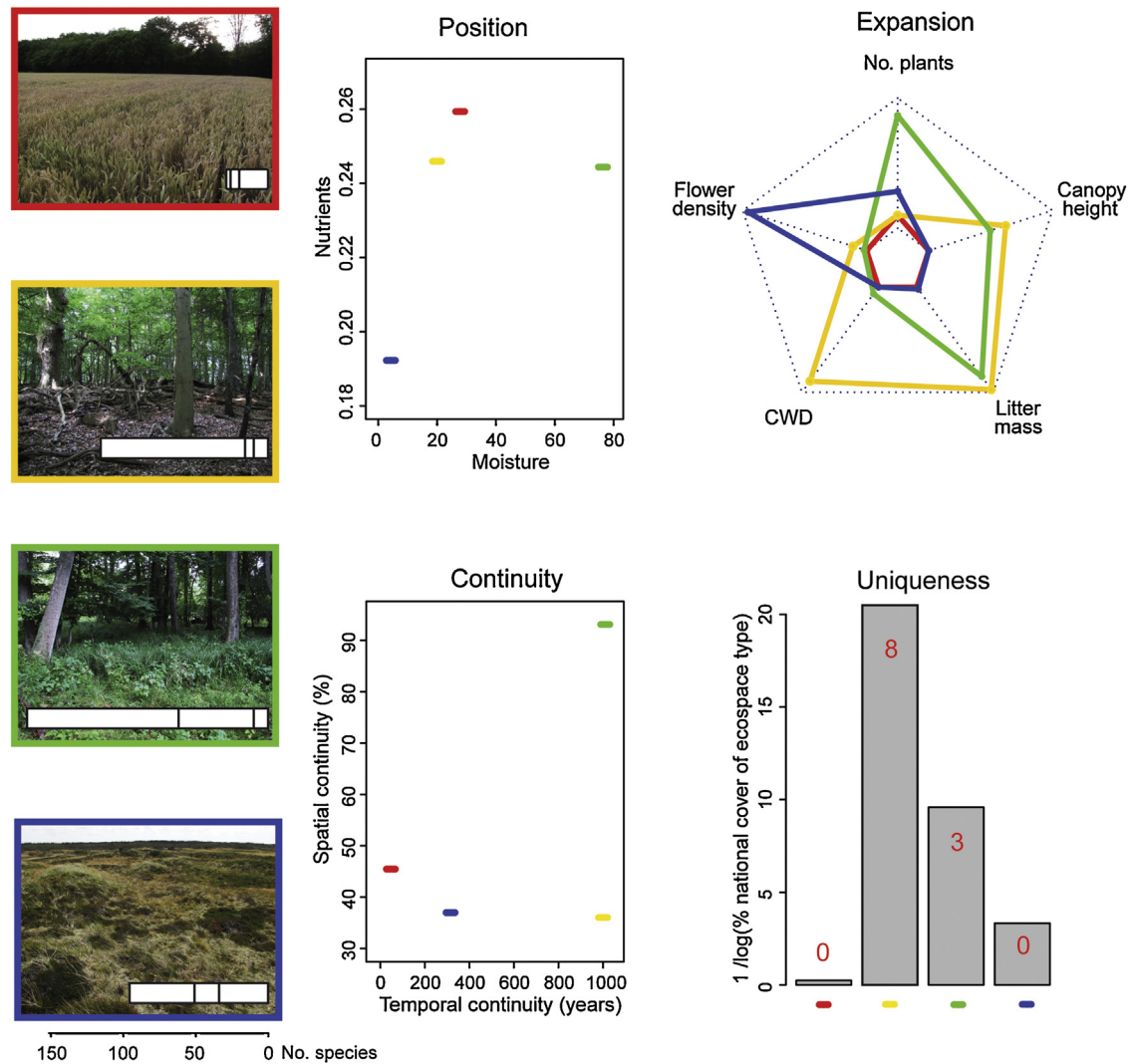

Fig. 1. Ecospace mapped empirically for four contrasted biotopes in Denmark, showing how biotopes may vary independently in position, expansion, continuity and uniqueness; and how that affects α-diversity. Red: arable field, yellow: dry, old-growth forest, green: swamp forest, blue: lichen-rich dune. Position is represented here by two important abiotic gradients: soil moisture (% volumetric water content) and nutrients (% leaf P). Expansion is represented by build-up of different carbon sources: i.e. flower density (range = 0–70/m^2), number of vascular plant species (No. plants; range = 0–60), canopy height (range = 0–8 m), litter mass (range = 0–150 g) and coarse woody debris (CWD; range = 0–50 m^3). Continuity is divided into spatial (% cover of the ecospace type within 500 m) and temporal continuity of the biotope (years since last major environmental change). The ecospace (position, expansion and continuity) effect on α-diversity is illustrated by the white bars on the photos representing the number of species found (divided into arthropods (right), plants (middle) and fungi (left)). Uniqueness is an estimate of the 'rarity; of the biotope at a larger scale estimated by 1/log (% national cover of ecospace type) of the given biotope. The higher the uniqueness, the more the biotope is expected to contribute to β-diversity, here represented by the number of red-listed species found in the four biotopes (red numbers). Photos: Lars Skipper.

biotope may be less clear and constant because of the continuous flow and mixing of resources, abiotic conditions, biota, etc.

Ecospace: the concept

Elton (1949, 1966) did not explicitly mention ecospace, but primordia of the concept are evident in the texts, stating that insect habitats may be defined abiotically, may be formed by host plants or parts of plants, or constitute localized structures, such as dung. Southwood (1978, 1996) explicitly discussed ecospace, but mainly used the concept to signify the physical surfaces livable from the perspective of small-bodied animals like insects. He estimated that the surface area of tree trunks, branches, twigs and foliage of a forest would be about 50-fold the soil surface below the canopy (Southwood 1978), and added that important components of ecospace still were to be included, such as the interior of living or dead plant parts. In this way, both authors briefly addressed the expansion of ecospace by living plants, but also touched upon other components. We take the idea a step further and propose to perceive ecospace as a general measure of the capacity of a given biotope to hold a certain assemblage and richness of species. We define ecospace explicitly for biotopes and with three constituent components: *position*, *expansion* and *continuity* (Fig. 1).

Past and present processes shape ecospace and translate ecospace into biodiversity, but ecospace itself is a state of the biotope, not a process. Species pools, from which biotopes are colonized, have been shaped by speciation, extinction, and migration – processes working at large temporal and spatial scales (Belyea & Lancaster 1999). Likewise, small-scale dispersal, colonization, stochastic dynamics and biotic interactions all contribute to populate a given biotope, with its ecospace acting as environmental filters (Hubbell 2001; MacArthur & Wilson 1967; Zobel 1997). A central assumption underlying ecospace as a unified framework for biodiversity research is thus that the ecospace can be mapped independently of the processes shaping the ecospace or populating the biotope, e.g. colonization can be assumed to take place if the ecospace is appropriate in terms of position, expansion and continuity. We do not attempt to cover variation in biodiversity between continents or biogeographical regions under influence of large-scale historical effects.

Ecospace – its basic elements and spatial extent

Position

Ecospace position reflects the position of the biotope in a (hyper-)space spanned by multiple abiotic gradients (Fig. 1). Position is the combination of biotope values for a number
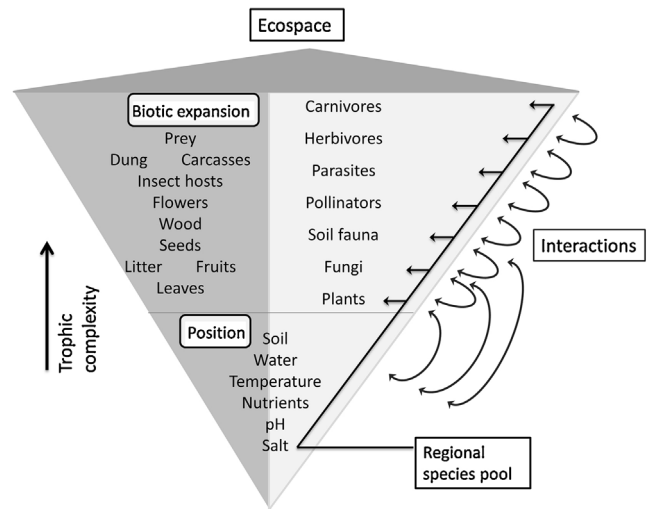

Fig. 2. Biotope ecospace is vertically organized along a trophic axis with biodiversity accumulating from the bottom to the top. At the bottom abiotic position provides resources and conditions for plant growth. First, plants expand ecospace, then herbivores and decomposers contribute to further expansion (diversification of organic carbon) and provide resources for zooparasites and predators. Regional species pools are filtered according to biotope position and dependence on lower trophic levels. Local dispersal, community assembly processes including biotic interactions affect the link between ecospace and local biodiversity in the biotope and also have a feedback effect on the regional species pool.

of continuous abiotic gradients, such as soil pH, nutrient availability, soil texture, soil moisture and temperature (e.g. Ellenberg et al. 1991) (Fig. 2). Homogeneity within the biotope is a prerequisite for a meaningful measurement of ecospace position represented by a set of common biotope values for abiotic condition. For some abiotic variables, e.g. temperature or soil moisture, extremes or temporal variation may be more relevant to define a position than the mean. Ecospace position resembles the abiotic niche but seen and mapped from the habitat perspective rather than the species perspective. We assume that a simple ecospace defined by a few abiotic factors may adequately predict species composition and significant parts of species richness (Dray et al. 2012). Position determines the abiotic filtering from a larger species pool (Van der Valk 1981; Wilson 1999; Zobel 1997) (Fig. 2), the size of which in turn depends on factors such as evolutionary history and historical bottlenecks (Bennett & Provan 2008; Eiserhardt, Borchsenius, Plum, Ordonez, & Svenning 2015; Jansson & Davies 2008). In Europe for example, high vascular plant species richness in alkaline soils has been proposed to reflect favorable conditions in evolutionary centers within floristic regions (Pärtel 2002), coupled with the putative extinction of more acidophilous species during Pleistocene glacial maxima (Ewald 2003). Although ecospace defines the filtering of the species pool and not its formation it has been suggested that local-scale processes driven by variation in ecospace position may even have had a

Fig. 3. Examples of biotic expansion by various carbon sources: Upper left: Plants as food source for herbivores, the specialist moth *Zygaena filipendulae* (Linnaeus, 1758) feeding on *Lotus corniculatus* (Linnaeus, 1758). Upper right: Flowers as a pollen and nectar source for the oligolectic solitary bee *Andrena hattorfiana* (Fabricius, 1775), feeding exclusively on *Knautia arvensis* (L.) Coult flowers. Middle left: Biotrophic interactions by three different fungus species forming ectomycorrhizae with roots of a deciduous tree. Middle right: The stump of a beaver-cut birch as habitat for the bracket fungus *Trametes versicolor* (Lloyd, 1921). Lower left: Dung as food source for the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758). Lower right: Carcasses as food source for a vulture, *Necrosyrtes monachus* (Temminck, 1823). Photo credits: Rasmus Ejrnæs (Zygaena), Jens H. Petersen (mycorrhiza), Thomas Borup Svendsen (Trametes), Morten DD Hansen (Andrena, Typhaeus), Rune Sø Neergaard (Necrosyrtes).

feedback relation to the buildup of the regional species pool (Bruun & Ejrnæs 2006), indicating a possible non-random link between position and species pool. Change in ecospace position can be caused by natural disturbances or succession as well as land-use change. Ecospace position may also feedback on processes, e.g. some positions are more likely to attract grazing or uprooting mammals (e.g. Bailey et al. 1996), some are more prone to wildfires (Cardille, Ventura, & Turner 2001), some intensify asymmetric resource competition between plants (Schwinning & Weiner 1998) and some may induce certain trophic interactions (Chase 1996). However, most natural processes are entirely or partly decoupled from the abiotic part of ecospace. For example coastal erosion, herbivory, trampling, defecation, flooding and strong winds may all take place across a wide range of different biotopes.

Expansion

The second component of ecospace is defined as the accumulation, formation and diversification of organic structures and substrates for species to live on and from (Figs. 1 and 2). Expansion consists of pools and structures of organic matter, ultimately derived from the autotrophic biota, and provides food, shelter and space for other species (Fig. 3). Consequently, expansion includes both the accumulation and spatial distribution of biomass (structural complexity of vegetation) and the partitioning of biomass into functionally separated carbon pools and structures (diversification of organic matter). Plant species richness, foliage, flowers (providing nectar and pollen), fruits/seeds, tree trunks, branches, dead wood, litter, carcasses and dung, all contribute to the expansion of ecospace providing substrates that heterotrophic animals and

fungi can live on or from (Figs. 1 and 3). While any biotope may be characterized by a quantified position along major abiotic gradients, expansion rather works by increasing the opportunities for species in the biotope. Certain elements of expansion may provide habitat for numerous species, for example c. 30% of the pollen-collecting bee species of Central and Northern Europe only collect pollen from a single plant genus (Pekkarinen 1997), 728 species of phytophagous insects are associated with *Salix* and 699 species with *Quercus* in Germany (Brändle & Brandl 2001), and more than 1500 species of saproxylic fungi are reported from Finnish forests (Siitonen 2001). While expansion may take place in response to the conditions given by ecospace position it can also be decoupled from position (e.g. pollen and nectar, coarse woody debris, dung and carcasses may occur almost independently of position, Fig. 3). Expansion is highly dynamic and challenging to quantify and predict compared to position, as some carbon pools – e.g. floral resources, dung or carcasses – are ephemeral, that is, they are hard to predict in space and time.

Elton (1966) acknowledged the importance of structure and organic resources provided by other organisms for the capacity of a biotope to support diversity. Although we use other terms, we agree that the diversity of resources provided by other organisms is a strong and often overlooked determinant of potential biodiversity. Each additional carbon pool and structure expands ecospace by adding new habitats and resources and potential α-diversity therefore increases with expansion. Expansion may be criticized for being impossible to quantify given the countless number of possible organic resources. We argue, however, that a limited number of parameters may adequately represent ecospace expansion, e.g., number of different plant species, variety of plant life forms, and availability of flowers, litter, dead wood and dung.

Continuity

Continuity refers to the extension in time and space of a given ecospace position and expansion (Fig. 1). Spatial and temporal continuity are estimated with respect to the biotope in question, but are measured for the surrounding area (spatial) and the conditions preceding (temporal) the current ecospace. Spatial and temporal continuity affect the colonization of a biotope (cf. meta-community theory, Leibold et al. 2004). Continuity in ecospace position enhances the probability of colonization and establishment of species from the species pool and decreases the risk of local extinction. We suggest a strict definition of temporal continuity per se, excluding the habitat formation time needed to develop e.g. veteran trees, charred coarse woody debris and diversity of carbon pools in the soil (Fretwell 1977, 1987; Nordén et al. 2014). With increasing continuity the realized species richness in the biotope approaches the potential species richness constrained by the regional species pool and the available conditions and resources.

Disruption of temporal continuity may happen due to major successional changes or abrupt disturbance. Disruption of continuity causes a change in ecospace position and/or expansion e.g. with wildfires, coastal erosion or land use change. For example cultivation for forestry or agriculture will disrupt the continuity of a natural level of expansion in a semi-natural grassland or old growth forest. Even if the abiotic position remains constant, the cultivation of crops enforces structurally uniform and species-poor vegetation (Whitehouse 2006). However, change in disturbance regimes in naturally disturbed areas will also lead to a loss of continuity (Kodric-Brown & Brown 2007). In this case, recurrent disturbance may be needed in order to maintain a given position and expansion (e.g. strong wind and sand transportation in white dunes, flooding in river beds, herbivory and trampling in grasslands).

Large scale diversity: the uniqueness of ecospaces

Given that ecospace can predict species composition, the contribution of a biotope to β-diversity (Tuomisto 2010) can be predicted by its uniqueness in position, expansion and continuity in the context of a larger geographic area (Fig. 1). Uniqueness is not part of the formulation of ecospace but should be regarded as an extrapolation of ecospace that enables us to assess the contribution of the biotope to the biodiversity of the surrounding landscape. Rare positions in ecospace will contribute more than common positions to the hypervolume of ecospace positions along a predefined number of gradients, and consequently may be an indicator of compositional turnover (β-diversity). Unlike position, organic carbon resources cannot be characterized by a mean value, but either take a binomial value (present–absent) or an abundance value (mass, cover, frequency). Therefore, expansion will contribute to uniqueness by the diversity of realized carbon pools. Similar to positions, carbon pools may be weighted by their rarity, so that rare pools such as coarse woody debris or species- and flower-rich biotopes count more than common pools. Different species groups may respond differently to ecospace variation, but we hypothesize that biotopes having unique positions and expansions in ecospace generally hold more unique species and thus contribute more to β-diversity at a landscape scale (Fig. 1). For this reason, even types of ecospace with limited expansion or representing positions with small associated species pools may contribute significantly to the total biodiversity if they represent rare positions or rare expansions, as can be recorded in e.g. raised bogs, sparsely vegetated sand dunes or biotopes with large carcasses. Spatial continuity and the uniqueness of an ecospace are related so that high spatial continuity normally implies low uniqueness of ecospaces among neighbor biotopes. However, the two elements are not reciprocal. For example, a regionally rare biotope may have high local

continuity – e.g. old growth forest patches in a national park. Similarly, a locally discontinuous biotope such as a woodland lot in an agricultural landscape may be regionally common.

Vertical organization of ecospace

Ecospace may be seen as vertically organized in a trophic hierarchy where biodiversity generally accumulates from the bottom to the top, with important positive top-down feedbacks (Fig. 2). At the bottom, we find the abiotic position providing resources and conditions for primary producers constituting the second level. At this level diversity will be determined by the abiotic environmental sorting of species from the regional species pool under influence by interspecific competition and temporal continuity (Belyea & Lancaster 1999). The plants expand ecospace by forming the living and dead organic carbon pools and biotic surfaces underpinning the megadiverse groups of heterotrophic organisms, i.e. animals and fungi (DeAngelis 1992). Further expansion takes place in response to biotic interactions. Herbivores, especially large herbivores, contribute by partial destruction of plant tissue (Bakker et al. 2015), transformation and relocation of plant litter and provision of dung, live animals and carcasses as resources for predators, parasites and decomposers.

To fully understand the link between ecospace and biodiversity, several – ideally all – species groups must be studied, because diversity patterns based exclusively on the sampling of one taxonomic group may differ markedly from other groups within the same biotope (white bars indicating species richness for different taxonomic groups in Fig. 1). Different aspects of ecospace are more important for some species groups than for others. Thus, limiting analyses to well-known or easily sampled taxonomic groups may blur important biodiversity patterns.

Applications, perspectives and caveats

According to classical niche theory (Hutchinson 1957), every species can be described by its fundamental niche: the hypervolume comprising all states of the environment allowing the species to exist. From a theoretical point of view, biodiversity could be studied and managed by considering the sum of all species' niches. In practice, however, the classic approach is intractable, even for small and relatively species-poor areas, because it requires estimation of niche parameters for all species in the species pool and interaction coefficients for all pairs of species. While the ecospace concept is compatible with the niche concept, it has a different scope. The ecospace concept refers to possible combinations of important ecological parameters without direct reference to limiting conditions or to interspecific competition (Bambach et al. 2007). Despite the obvious advances to be gained in studies of relationships between selected taxonomic groups

and simple underlying gradients (e.g. Grace et al. 2016 for productivity and plant richness), a unifying multi-taxon approach to describe and fully understand the variation in biodiversity is needed. The justification for ecospace as a new framework for studying variation in biodiversity lies in its conceptualization of all major aspects of a biotope needed to understand its capacity to support populations of species. Ecospace includes the role of abiotic gradients, biotic resources and spatiotemporal continuity. Thus, it opens for an integration and comparison of e.g. environmental filtering and biotic interactions along environmental gradients (Keddy 1992; Kraft, Valencia, & Ackerly 2008) and neutral processes according to the rules of island biogeography (Hubbell 2001; MacArthur & Wilson 1967). On top of these points, we add expansion as the build-up and diversification of pools of organic carbon providing an essential niche-space for megadiverse taxonomic groups such as arthropods and fungi. Despite the obvious contribution of these taxa to terrestrial biodiversity, they are rarely covered extensively in biodiversity studies, mainly because they are too difficult to identify and too resource demanding to record. This situation may change in the near future given the rapid development of metagenomics (Coissac, Hollingsworth, Lavergne, & Taberlet 2016). We acknowledge the scale-dependency of biodiversity (Colwell & Coddington 1994; Levin 1992) by suggesting uniqueness as a biotope-scale metric for the contribution of the biotope to the biodiversity of the total landscape in which it is situated. Uniqueness is not itself part of ecospace, but rather meant as a link from ecospace driven variation in α-diversity and biotic composition to β- and γ-diversity – particularly important in conservation planning (Brooks et al. 2006). But also, and perhaps more importantly, the ecospace approach urges researchers to search for the simplest possible explanatory model of variation in biodiversity, pruning away all redundant or inferior variables. We recommend taking the full model as starting point and reducing this in a search for maximum parsimony.

We have deliberately defined ecospace to describe a measurable state and excluded processes such as disturbance and succession. This makes a difference to approaches using processes to predict variation in species richness or composition, e.g. the intermediate disturbance hypothesis (Grime 1973) or the disturbance axis in the CSR-classification of plant strategies (Grime 1977). This said, we would very much encourage research in the biological processes required to fill, clear, change, expand or share a given ecospace.

In the palaeoecological community, a similar concept of ecospace has been developed and advanced, in which ecospace signifies the potential and realized modes of life for a prehistoric marine fauna (Bambach 1983; Bambach et al. 2007). While emphasis is on the mapping of life modes as proxy for ecospace filling, the basic idea is fully compatible, namely that resource availability and abiotic conditions in the ecosystem constrains the possible modes of life, and also that diversity begets diversity, just as is the case with biotic expansion (Bambach et al. 2007).

Ecospace may also be applied as concept in nature conservation. At the biotope scale, managers can consider ways to promote ecospace expansion or to restore a more natural ecospace position. Likewise, conservation planning can target spatiotemporal continuity in prioritized localization of protected areas within landscapes. Ideally, managers can map elements of ecospace without full biotic inventories reducing costs without sacrificing meaningful conservation targets. Ecospace may also be useful as evaluation metric in open-ended management, where the target cannot be specified in terms of a particular set of species. Current conservation management almost invariably targets conspicuous or easily mapped groups of species, such as mammals, plants and birds (EU Birds Directive 1979; EU Habitats Directive 1992; Ricketts, Dinerstein, Olson, & Loucks 1999), despite the fact that fungi and insects constitute the vast majority of species richness.

We are well aware that the value of ecospace as a framework for ecological research and nature conservation can only be assessed by extensive testing against comprehensive empirical data. We therefore invite fellow scientists and conservationists to join us in testing and revising the concept and to contribute to the research in ecospace, underlying drivers, and the resulting biodiversity.

Acknowledgements

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